ON THE SUPPOSED ANTAGONISM OF MENDELIAN TO BIOMETRIC THEORIES OF HEREDITY

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On the Supposed Antagonism of Mendelian to Biometric Theories of Heredity

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I*

DISSENSIONS IN SCIENTIFIC MATTERS may be said to be of two kinds, of which one is a disagreement about fact, and can be settled by an appeal to fact, while the other is the conflict of theoretical interpretations which cannot be so easily concluded. When Owen said that an ape's brain had not a hippocampus minor and Huxley asserted that it had, Flower announced that he had an ape's brain in his pocket: and the dissection of the brain put an end to the discussion. But in the second form of controversy no such touchstone can be applied, and in the debate on heredity at Cambridge this year Mendelian maize-cobs were displayed in vain. Of this kind of controversy there are again two sorts, one in which the theories put forward by the opposite factions are mutually exclusive, and another in which while there is apparent incompatibility the truth of both of the hypotheses is ultimately demonstrable. It remains to be seen to which of these subdivisions the Cambridge debate[†] and the wider discussion of which it was the

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^{*} This essay is so arranged that if the reader is not interested in the phenomenon of hybridization he may leave out Part II.

[†] Reported in *Nature, Vol.* 70, pp. 538 and 539.

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outcome, are to be assigned. If the two theories are mutually exclusive, which is right? If on the other hand they are not, how do they fit in with one another? These are questions which "the general enquiring public" may be expected to ask and to which the specially trained biologist may be expected to supply an answer.

It is the thesis of the present essay to demonstrate the compatibility of Mendelian and biometric theory and to account for their apparent antagonism.

A few words as to the spirit and scope of this essay seem to me to be necessary. There are two methods of scientific criticism, if indeed one of them can be justly called scientific. One arises from a determination to crush a theory, while the other consists in the postponement of the attack until every endeavour has been made to appreciate the exact point of view of the upholders of that theory, and in a willingness to put off the attack for ever if the theory should not be found wanting after all. The most flagrant example of the first kind of criticism, on which I can lay hands, flowed from the pen of a writer who, after having misrepresented the theory he was attacking by declaring that it was "an essential part of the Mendelian hypothesis that the (so-called 'extracted') recessive individual which is produced by pairing two first crosses, is in every respect similar to the original pure recessive,"* concludes with these words: "This mouse is clearly not a pure dominant, because it produces albinos; it is not a dominant hybrid because it has pink eyes; and it cannot be a recessive because when paired with an albino it produces some black-eyed forms." It is evident from this quotation that the stimulus which actuated the author was a desire to stultify and refute Mendelian theory at all costs, and that he did not make the smallest attempt to discover what Mendelian theory really was or to put himself in the position of those who held it to be true. For an example of the second form of criticism I suggest that the reader may turn to the following pages: in them I shall do my best to discover the most essential characteristics of Mendelian and biometric theory and so to put myself in a position to discuss their mutual relationship.

With regard to the scope of this essay, there is one point I wish to emphasize: it may be that some critic will lay down this pamphlet with the remark that all that he has read may be very true, but that the fact remains that the only thing which "matters" is the mass-phenomenon; or another may declare that the key which will unlock the secret of heredity can only be obtained by a study of the properties of the germ

^{*} A. D. Darbishire, *Biometrika*, Vol. II., pp. 282 and 285.

cells. I do not propose to express an opinion on either of these contentions, but I wish most strongly to insist that when a man has made either of them, he has stepped from one country into another. After discussing the mutual relation of two theories, he suddenly asserts that after all it is only one of them that matters — as one who during a discussion of the evidence for and against the existence of mental activity after the death of the brain should declare that after all, belief in such a survival was a great comfort to many: both questions may be worth discussing, but they should be discussed separately. In this essay I propose to treat of the mutual relations of the two theories purely as theories, without touching on the question of their possible value to the pure or applied biologist.

The reader may easily convince himself by a perusal of the literature on this subject that the self-same facts are interpreted by the rival schools of thought in the light of their own theories: and if he looks for recognition from either party that there may be something of truth in the opinions of their opponents, he will search in vain. I do not propose to discuss the opposite points of view, because I believe that the remedy for the present inconclusiveness of the discussion lies very deep, and is to be found in the clear appreciation of the fundamental relation between the biometric and Mendelian points of view.*

II.

At a time when I did not clearly see this relation, I had before me some data which convinced me that the Mendelian interpretation of the phenomenon of segregation was wrong, and that the facts were striking evidence of the truth of Galton's theory.

There are two attributes of a heterozygote which are said to follow from the theoretical constitution of its gonad; one is that a quarter of the population produced by the union of heterozygotes consists of individuals bearing the recessive character; and the other is that half the population produced by mating heterozygotes with recessives consists of recessives. My hybrids[†] were tested for these two properties and the results were not denied to be in accord with Mendelian expectation. But this result was not conclusive in favour of that theory only, because the proportion of recessives demanded by Mendelian theory in the case of

^{*} The reader who wishes to follow the discussion of the facts at first hand will find the necessary references to four cases in the Appendix.

[†] Biometrika, Vol. III., pp. 30-33

the first property was identical, and in the case of the second only slightly less than that which follows from the truth of Galton's generalization.*

The Galtonian prediction of the number of albinos that will be produced by two hybrids (H) each of which is the offspring of a purebred waltzing and a pure-bred albino mouse is .25 of their generation; while on that theory the proportion of albinos in a generation resulting from the union of hybrids with albinos (A) is .53125, if we only calculate as far back as the great-grandparental generation.

We have seen, therefore, that hybrids were mated with hybrids, and that they were also mated with albinos. In this way two kinds of hybrids were produced which could not be distinguished from one another by their outward appearance but differed in the amount of their albino ancestry; for while the one kind, which we may call HH, resulted from the union of two hybrids, the other, HA, was the offspring of a hybrid and an albino. I took those individuals to be hybrids which resembled the first crosses (F_1) in coat and eye colour, *i.e.*, in the possession of a coloured coat and pigmented eye.

In mating hybrids of this generation (F_1) I did not previously look up their ancestry in books containing their genealogical record, so that mice of the categories HH and HA were mated at random: in this way three kinds of crosses were made $HH \times HH$, $HH \times HA$ and $HA \times HA$. In each type of union a hybrid was mated with a hybrid, as I believed at the time: and as on Mendelian theory there is no difference between the gametic constitution of DR produced by $DR \times DR$ and DR with parentage DR \times RR, I argued[†] that, if that theory were true, each type of union would produce a fraternity, half of which would be composed of hybrids, a quarter of which would be composed of pink-eyed mice with coloured coats, while the remaining quarter would consist of albinos; on the other hand, it was evident that on Galton's theory of heredity the proportion would not only not be the same in each of the three cases but would differ in direct proportion to the amount of albino blood in the parents of the population. The subjoined table gives together with the actual result, the proportions of albinos as predicted by the two theories: in calculating the Galtonian prediction I have not taken into account any generations more remote than the great-greatgrandparental.‡

^{*} Francis Galton, Proc. Roy. Soc., Vol. 61, p. 402, line 13.

[†] Biom, Vol. III., pp. 23-25.

[‡] I thank Mr. J. T. Wadsworth for checking this simple calculation.

Type of Parentage	Number of Young	Mendelian Expectation.	Galtonian Expectation.	Actual Result.
$\mathrm{HH} imes \mathrm{HH}$	93	25%	9.37%	10.75%
$\mathrm{HH} imes \mathrm{HA}$	107	25%	17.96%	18.69%
$\mathrm{HA} imes \mathrm{HA}$	121	25%	26.56%	24.79%

Before continuing my argument, I should like to dwell for a little on the circumstances which led me to believe that I was dealing in F_2 with hybrids and indeed with heterozygotes in the strict Mendelian sense of the term. In the first place these putative hybrids bore the same features of coat and eye colour as the F_1 hybrids exhibited; secondly, they formed 50% of the F_2 generation, and lastly at least two upholders of Mendelian theory^{*} had asserted that the heterozygote was represented in my experiment by the coloured mice with pigmented eyes.

To resume the thread: these results were brought before the notice of a student of heredity whose first question was, if there had ever resulted from the union of two hybrids a family in which there were no albinos; a query to which an affirmative answer was given. Then the following argument was used by my critic: 'The only proof that a given individual is a hybrid is one which is based on an examination of its gametic constitution; in the case of your mice you have no right to say that a grey mouse with black eyes is a hybrid until you have mated it with an albino and obtained albino young in the litter thus produced: until this has been done there is no evidence that it is not a dominant. In the case you have just shewn me you mated coloured mice with dark eyes without making this test, and by this neglect many dominants may have been included among them, and you see that this suggestion, against the truth of which you have no evidence, accounts just as well as Galtonian theory for the difference in the proportions of albinos in the three kinds of coatings.' I replied that the test of the true heterozygote nature of the apparent hybrids should be made though I did not believe the suggested Mendelian interpretation of this apparently conclusive anti-Mendelian result.

The test has been applied with the most remarkable result: but before giving an account of it I propose to describe my reasons for adhering to the interpretation of the facts of this case which I held at first. I believed that all the individuals in F_2 with pigmented coats and eyes were hybrids and that when mated with albinos they would all of them give some albinos; that the hybrids of F_2 differed from those of F_1 only in degree, namely that, while it was the property of the latter when

^{*} Castle and Allen., Proc. Amer. Acad. Arts and Sci., Vol. 38; No. 21

mated together to produce as nearly as possible one albino in every four in their litters, the former had a less albino-producing capacity; and that the hybrids of F_2 would each be capable of producing still fewer albinos and so on with succeeding generations. My belief was that the hybrids of a given generation, say F_5 , would be all the same with regard to their albino-producing capacity, but would differ from those of F₄ in having a smaller one. Before dealing with the origin and meaning of this view I will relate how, by the application of the test suggested, it was shewn to be erroneous. The test of the real heterozygote nature of the hybrids was made, as suggested, by mating them with albinos. In all cases but two I found as I had expected that albinos were produced and I ascribed the absence of albinos from the other two litters to chance. and had no doubt that I had only to mate them with albinos again to obtain the required proof of their hybridity. But the next litters from the two mice, mated thus, contained no albinos. So that it began to look very much as if these apparent hybrids really were dominants. This fact in itself pointed to the truth of the suggestion that mice with coloured coats and eyes were of two kinds - hybrids and dominants; but coupled with the result of mating the gametically tested hybrids *inter se* it afforded fairly complete confirmation' of that hypothesis, for of the 92 young resulting from such union, 14 had a pink eye and coloured coat, 58 a dark eye with coloured coat, while 20 were albinos.

I wish particularly to remind the reader that I do not think that these numbers are large enough to draw any numerical conclusions from; they are introduced solely as part of an argument which is intended to shew how I came to see that the facts summarized in the Table on p. 5, were equally in accord with Mendelian and Galtonian theory and their value in this respect will not be in the least impaired if it ultimately turns out that the proportion in which the three categories of coat and eye colour occur are "in every respect discordant with" Mendelian prediction.

That the two mice which gave no albinos in the two matings referred to *really* are dominant is, I think, placed beyond doubt by the fact that in a third mating with albinos they have failed to produce anything but coloured mice with black eyes.* That the remaining mice are heterozygotes is also beyond doubt, and that a quarter of the population produced by breeding them together is composed of albinos remains to be demonstrated. The Table on p. 5 therefore is in no wise a refutation of Mendelian theory; at any rate the suggested Mendelian interpretation of the facts cannot be regarded as disproved.

^{*} Besides these two mice which have been tested thrice there are three which have been tested twice, two bucks and a doe, with the same result.

Nevertheless the facts are no less in accord with Galtonian theory, though in a different way than I at first held: the manner in which I believed that the truth of that theory would be borne out was as I have said before, and as I wish to emphasize again, by the gradual diminution of the albino-producing capacity of each hybrid of successive generations. It now appears that the manner in which that theory is borne out by these facts is by the gradual invasion of the 'hybrid' ranks in successive generations by dominant individuals bearing the external hybrid characteristics whether there will appear among the 'dominants' or even recessives a compensating number of hybrids, or even whether this is demanded by Mendelian theory is a question of fact which does not affect my argument. What I want to point out is that I fell into the error of believing that that which was true of the whole population was also true of the individual — a mistake which, I believe, was due to an attempt to discover whether certain phenomena were evidence in favour of the one or the other of two theories without appreciating the essential character of either theory and much less their mutual relation; to a failure, in short, to realise that a biometric formula of heredity is true only of large masses, the component units of which in most cases unite at random, while the Mendelian theory is an attempt to account for the hereditary phenomena exhibited by the union of individuals carefully selected, by a theory of the constitution of their germ cells. It is perhaps not unnatural, though it is certainly unjustifiable, that, when an experimenter is thinking of a set of facts before him now in terms of the one theory and now in terms of the other without having clearly fixed the peculiar characters of each theory to its proper owner, he should get these characters misplaced, that he should add to the real character of the biometric theory one which it does not possess - that of applicability to the individual. I have discussed this particular error of judgment at some length because it illustrates the kind of mistake a student of heredity at the present time may make unless he realises the exact nature, at which I have so far only hinted, of the two theories whose compatibility with fact he is testing. Were I not persuaded that mine is not the only case in which this or a similar kind of error has been made I should not have described it: and it is because I believe that the misunderstandings and arguments at cross purposes, which have lately characterized discussions on heredity, will be things of the past when the relation between biometric and Mendelian theory is clearly seen that I set forth the following considerations.

From a point of view which commands a wide range of our experience, our knowledge may be divided into two distinct classes, according as we are dealing collectively with a vast number of things — with a mass phenomenon; or with the individual units which make up that mass. These two kinds of knowledge are radically different, and are distinguished from one another by the same characters as those which are peculiar to the two meanings of the statement that a thing happens by chance; for when we make this statement we may either be referring to the method by which I decided whether to write 'biometric' or 'Mendelian' first in the title of this paper, or to the result of a very great number of tosses — an approximation to 50% heads and 50% tails, which is close in proportion as the number of trials is great. The first difference that I mention between these two meanings of chance. as illustrative of the characters of the two classes into which we have divided our aspect of things, is that, while in the case of the first it is impossible to predict the result of a single trial, there is nothing easier to foretell than the result of a very large number; nothing is more uncertain than the former, nothing more certain than the latter. A second difference between these two groups is that that which is true of the mass is not necessarily true of all the component individuals, though it may be of some: in the case of coin-tossing, the statement that the result of an infinitely large number of trials is an equal number of heads and tails is contradicted at every single toss, though this would not be the case if some of the coins we tossed had half the head and half the tail on each side of the coin.* Is it necessary to add that from the fact that what is true of the mass is not true of the individual it does not follow that assertions about the individual are antagonistic to statements about the mass? It is important to realise this truth because it is seldom done and apparently difficult, the difficulty resulting from the extreme difference of the two points of view. A midge walking across a picture of a meadow done by the three-colour process would assert that it was traversing a white plain, over which were distributed patches of different sizes and three colours, red, blue, and yellow: a child would maintain that it was walking across a picture of a field; each would be convinced that he was right and the other wrong; yet that both were

^{*} I have found Galton's apparatus for illustrating the origin of the curve of frequency (*Natural Inheritance*, p. 63, *Fig.* 7) very useful for explaining the difference between these two classes. An example of the first is afforded by allowing a single shot to run down the inclined board; an example of the second by displaying the result of a thousand such events.

right could be recognized by any man able to use a magnifying lens. This leads us to a third feature of the relation between our two classes, (which results from the fact that our knowledge has probably developed along those lines that our point of view has made most valuable), namely, that in proportion as our knowledge of the component units is small so is our knowledge of the mass result great.

To take an example of these two ways of looking at things. The climate of a country or long period of time is a mass-phenomenon: the particular climatic condition of a certain day is referred to as the weather.* It is, though it may be becoming less, impossible to predict the weather with precision: but the nature of the climate of a given country or long period of time is a matter of tolerable certainty. Yet the statement that the summer is warm does not exclude the possibility of a frost in May. That our practical knowledge of the elements is confined to the climate is evident from the fact that, having procured, we begin to put on warmer clothing at a certain, period of the year: but if our intelligence were so sharpened, or our meteorological instruments so improved that we could predict the exact state of the weather a fortnight in advance, we should not procure the warmer raiment until we knew that it would be needed.

Another phenomenon which may be looked at from these two points of view is that of the causation of heat: it is believed that the heat of a substance is occasioned by the mean speed at which the molecules of which it is composed are travelling. To deal with the three differences between our two aspects of things in turn; it is evident first that, while our ignorance of the speed of an individual molecule is so great that we try to conceal it by saying that it is determined by chance, our knowledge of the average speed of myriads of them is so accurate that certain laws of thermo-dynamics have been formulated. Secondly, it has been calculated that a curve representing the frequency of the various speeds spread over the molecules is an ordinary curve of error; so that although that which is true of the mass is also true of some of the molecules, it is by no means true of all of them. Thirdly, the only point of view from which we can regard this phenomenon at present is that from which we can only discern the mass-result: but that it is by no means inconceivable that there may be another point of view is evident

^{* &}quot;By *climate* we mean the sum total of the meteorological phenomena that characterize the average condition of the atmosphere at any one place on the earth's surface. That which we call *weather* is only one phase in the succession of phenomena whose complete cycle, recurring with greater or less uniformity every year, constitutes the climate of any locality." P. 1. – J. Hann's "Handbook of Climatology," transl. by R. de C. Ward, 1903.

to all who are familiar with Clerk Maxwell's demon, a being who is so essential to my argument that I shall make no apology for quoting his creator's description of him in full: "One of the best-established facts in thermo-dynamics is that it is impossible in a system enclosed in an envelope which permits neither change of volume nor passage of heat, and in which both the temperature and pressure are everywhere the same, to produce any inequality of temperature or pressure without the expenditure of work. This is the second law of thermo-dynamics, and it is undoubtedly true so long as we can deal with bodies only in mass, and have no power of *perceiving or handling the separate*^{*} molecules of which they are made up. But if we conceive a being whose faculties are so sharpened that he can follow evey (sic) molecule in its course, such a being, whose attributes are still as essentially finite as our own, would be able to do what is at present impossible to us. For we have seen that the molecules in a vessel of air at uniform temperature are moving with velocities by no means uniform, though the mean velocity of any great number of them, arbitrarily selected, is almost exactly uniform. Now let us suppose that such a vessel is divided into two portions, A and B, by a division in which there is a small hole, and that a being who can see the individual molecules, opens and closes this hole, so as to allow only the swifter molecules to pass from A to B, and only the slower ones to pass from B to A. He will thus without expenditure of work, raise the temperature of B and lower that of A, in contradiction to the second law of thermo-dynamics."

The point of view of the demon is so different from that of the physicist that one of the truest generalizations of the latter would be declared absolutely false by the former: yet no one remains blind for a moment to the fact that the contradiction of their respective statements is only apparent, and is due to the radical difference in their points of view.

Now I believe that the difference between the point of view of the Mendelian and the biometrician is very like the difference between that of the demon and that of the physicist. The biometrician, with a new weapon of observation, is only concerned with mass phenomena; the individuals which go to swell his correlation tables are, like the atoms of the physicist, units of which no knowledge is required to attain the result at which he aims. But I need not dwell on the exactness of the parallel when we have these words from "the inventor of the term biometry[†]" : — "*Our knowledge of atoms and our application of

^{*} My italics.

[†] Nature. Oct. 27, 1904. P. 626.

atomic and molecular hypotheses to problems in heat, elasticity, and cohesion is essentially based on statistics of average conduct. Corpuscles in each other's presence are supposed to obey certain laws of motion, but no explanation has hitherto been given of these laws. So it is with vital units; they vary, why they vary we know not, and we *explain* nothing by attributing it to bathmic influences. As we can predict little or nothing of the individual atom, so we can predict little or nothing of the individual vital unit. We can deal only with statistics of average conduct. We have laws of variation and laws of heredity, in themselves quite as general and as definite as the majority of those we meet with in physics."

I may perhaps take this opportunity to explain that I have used the term biometric theory advisedly, and that the definition of it that I have had before my eyes is not merely "the application of exact statistical methods to the problems of biology,"[†] but the aspect of vital phenomena, just quoted from the "Grammar of Science," which prompts that application.

And I believe that I am justified in including under the term "biometric" both Pearson's and Galton's theories which, though in one respect they are radically different,[‡] resemble each other in regarding heredity as a mass-phenomenon and in treating it by the statistical method.

The Mendelian, on the other hand, with a new application of experiment, is a biological demon who, "perceiving" and "handling the separate" units themselves, tries to find out their properties by mating them with other units. But, here again, I need not expatiate on the closeness of the parallel I have suggested when we have these words from the champion of Mendelism in this country[§]: — "In the Mendelian method of experiment the one essential is that the posterity of each *individual* should be traced separately. If individuals from necessity are treated collectively, it must be proved that their composition is identical. In direct contradiction to the methods of current statistics, Mendel saw by sure penetration that masses must be avoided."

There is one direction in which my parallel may seem at first sight to be incapable of being pushed very far; it may be urged that we never

^{*} Karl Pearson. "Grammar of Science," 2nd Ed., pp. 500 and 501.

[†] Nature. Oct. 27, 1904. P. 626.

[‡] Karl Pearson. *Biometrika*. Vol. III., pp. 110 and 111.

[§] Presidential Address to Section D, Brit. Assoc., 1904, in *Nature*, August 25, p. 409.

can have any knowledge of the individual, but only of kinds of individuals, because in single cases it is impossible to eliminate the attributes which are due to chance: so that Mendelian methods are more to be compared with chemistry, which tests the property, not of units, but of masses of units which are known to be all the same.^{*} But this fact does not in the least lessen the closeness of the parallel, for we have no reason to believe that the demon, if his attributes are as "essentially finite as our own," would have or need any knowledge of the individual molecules, but merely the ability to classify them into — say — ten classes, ranging from very fast to very slow, and to close his door according to their speed and direction. This point does not seem to be of much importance, but I did not wish, by not referring to it, to appear to have overlooked it.

One result, which seems to me to follow naturally from the truth of my comparison, is that it is unreasonable to apply, as has often been done, the criteria of either theory to a set of facts in which the conditions, on which that theory is true, do not obtain; and the manner in which materials for the study of heredity are collected by Mendelians is so different from those employed by biometricians that this is very rarely, if ever, the case.

From this it follows that the naturalist who sets out to attack the problem of heredity will not as in the past collect his facts and then see whether they fit the one theory or the other, but will make it his first duty to decide whether he will attack it from the point of view of the physicist or the demon, from the outside or from the inside. If he decides on the former, he may if he wishes, breed his material, but he will find a great deal ready to hand in the records of matings of, for example, grey-hounds, racehorses, and men. If he decides on the latter, it is almost indispensable that he should breed his material for himself. That is why biometricians are concerned with 'ancestry,' and Mendelians with 'posterity.' Yet these are not two things, but one thing, looked at from opposite ends. But there is a difference between ancestry and posterity, namely that the latter only can be dealt with by the method of experiment.

A confirmatory sidelight on the truth of my comparison is thrown by the consideration that of the two men whom I have quoted as representing the rival theories of heredity, the biometer is a mathematician, while the Mendelian is a zoologist: and it is entirely in accord with expectation that the former regards the phenomena of

^{*} Cf. "The breeding-pen is to us what the test-tube is to the chemist" — same Address, p. 409, 1st column; and cf. Reports to Evol. Com. Royal Soc., I., p. 159.

heredity from that point of view which does not presuppose knowledge of the unit, while the latter is concerned with the properties of the individual organism.

If we could imagine the demon and the physicist incapable of appreciating each others point of view we could understand the contempt each would have for the clumsy methods and erroneous opinions of the other.

And though we can perhaps understand the Mendelian declaring as he slides the latch of his breeding-pen that "Operating among such phenomena the gross statistical method is a misleading instrument; and, applied to these intricate discriminations, the imposing Correlation Table into which the biometrical Procrustes fits his arrays of unanalysed data is still no substitute for the common sieve of a trained judgment;" and that "nothing but minute analysis of the facts by an observer thoroughly conversant with the particular plant or animal, its habits and properties, checked by the test of crucial experiment, can disentangle the truth;"* and appreciate the point of view of the Biometer marshalling his vast arrays when he contends that it is "better to use the purely descriptive statements of Galton and Pearson than to invoke the cumbrous and undemonstrable gametic mechanism on which Mendel's hypothesis rests,"[†] I do not see that we have any right to remain blind any longer to the fact that the contradiction of their respective theories is only apparent, and is due to the radical difference in their points of view.

^{*} Pres. Address to Sect. D. Nature, August 25, 1904, P. 408.

[†] Nature, Sept. 29, 1904, p. 539.

APPENDIX.

Facts.	Mendelian Interpretation	Biometric Description
"Versuche über Pflanzen- Hybriden," by Gregor Men- del. Verhandl. naturforsch. Ver. in Brünn, vol. 4, 1865. Abhandl. p. 1. Transl. into Engl. in "Mendel's Principles of Heredity," by W. Bateson.	 (i.) Mendel, G., p. 72 in Engl. Transl. by Bateson. (ii.) Bateson, W. Mendel's Principles, p. 57 et seq. 	Weldon, W. F. R. <i>Nature</i> , vol. 70, p. 539.
"Versuche mit Kreuzungen von verschiedenen Rassender Hausmaus," by G. von Guaita. <i>Ber. d. naturforsch. Gesell.</i> <i>Freiburg, x.,</i> 1898, p. 317. Zweite Mitth., etc., <i>Ibid.</i> xi., 1900, p. 131.	 (i.) Bateson. W. Proc. Zool. Soc., 1903, vol. ii., p. 86–88. (ii.) Castle, W. E. Proc. Amer. Acad. Arts and Sci., vol. 39, no. 8, p. 231, Table II. 	
"L'Hérédité de la Pigmentation chez les Souris" (3 ^{me} Note), by L Cuénot. Arch. De Zool. Exp. et gén. 1904 (4), vol. 2. Notes et Revue, no. 3. pp. 45–56.	Cuénot, L. loc. cit.	Weldon, W. F. R. <i>Nature</i> , vol. 70, p 539.
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